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A review of the occurrence and ecology of dense populations of *Ditrupa arietina* (Polychaeta: Serpulidae)

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Abstract

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Dense populations of the free-living serpulid *Ditrupa arietina* were first recorded to the west and north of the Shetland Isles in the 1920s and have since been reported from the Celtic and North Seas, the Armorican shelf, the Mediterranean and the Azores. These dense populations (of many thousands per square metre) numerically dominate the benthic fauna, and the tubes provide sites of attachment for a range of other species. Vacated tubes are also occupied by other animals, and tube fragments can contribute significantly to biogenic carbonate sediments, both Recent and fossil. Dense *Ditrupa* populations have been the subject of detailed autecological research over the last 15 years, but in spite of the apparent ecological importance of the species, it is not reflected in the European Nature Information System (EUNIS) or other North-east (NE) Atlantic habitat classifications. This paper provides a synthesis of the environmental conditions where high densities of *Ditrupa* have been found, with new data from seabed samples and photos. *Ditrupa* appears to occupy different habitats in the NE Atlantic and the Mediterranean, and studies of its morphology and genetics are needed to determine if there is a taxonomic basis to this ecological separation. Although the evidence is sparse, it is concluded that, in the NE Atlantic, dense populations of *Ditrupa* are found in areas where the seabed is periodically disturbed by internal wave action. European and other habitat classification schemes require revision to reflect the areas of occurrence and benthic effects of internal waves.

Keywords

polychaete, North-east Atlantic, Mediterranean, faunal assemblage, habitat classification, EUNIS, disturbance, internal waves

Introduction

The free-living serpulid polychaete *Ditrupa arietina* (O.F. Müller, 1776), was described from material probably from Norway or Denmark (ten Hove and Smith, 1990). Until 1990, it was generally considered to have a cosmopolitan distribution; ten Hove and Smith (1990) clarified the taxonomy of the genus and concluded that the distribution of *D. arietina* was boreal to subtropical East Atlantic. The genus is of geological importance, with extensive fossil deposits (see, for example, Dominici, 2001 and Martinell et al., 2012) and makes significant contributions to some Recent biogenic carbonate sands and gravels (see Wilson 1979, 1982). Ecologically, the tubes provide sites of attachment for other taxa, including solitary corals, other serpulids, foraminiferans and bryozoans (see McIntosh, 1923; Wilson, 1976), while vacated tubes are occupied by a range of animals (see Myers and McGrath, 1979; Wilson, 1982). Predators of the species are poorly known, with the exception of flatfish (Rae, 1956) and naticid gastropods, which leave characteristic drill holes (Grey et al., 2005). The species can achieve very high densities (~11,000/m^2) (Grémare et al., 1998) and has been listed as characteristic of some benthic assemblages (e.g. Stephen, 1923; Glémarec, 1969; Labrune et al., 2007a) although it is not listed in any assemblage in EUNIS (European Nature Information System), a pan-European classification of marine, freshwater and terrestrial habitats (http://eunis.eea.europa.eu/about.jsp). This review of the occurrence of dense populations of *D. arietina* and whether it is a characterising species of particular habitat types was prompted by finding the species in great abundance during a regional survey of the northern North Sea, within a faunal assemblage that closely matched that described by Stephen (1923).

Benthic assemblages characterised by high densities of *Ditrupa arietina*

Fig. 1 shows the distribution of records of high densities of *Ditrupa* from the North-east (NE) Atlantic and Mediterranean (where positions or maps were given), and for convenience the records are summarised below by geographic area. Greater emphasis is placed on the NE Atlantic records (including previously unpublished data) as a series of recent papers describe and discuss the occurrence of high densities of *Ditrupa* in the Mediterranean.

NE Atlantic records of high densities of *Ditrupa arietina*

The first quantitative benthic study to report high densities of *Ditrupa* was by Stephen (1923, as *Ditrupa subulata* = *arietina*). He sampled extensively across the central and northern North Sea and to the west of Scotland using a Petersen grab and an ~1.5mm sieve. Stephen (1923) distinguished a series of faunal community types, including a *Ditrupa* community to the north and west of Shetland with two variations: pure *Ditrupa* (at up to 720/m^2 cited in the text and 360/m^2 listed in Table VI) described as "very barren with few other forms being found where it occurs", and *Ditrupa* with *Ophiura affinis*, described as "a mingling of *Ditrupa subulata* with the *Ophiura affinis* community". McIntosh (1869) had earlier noted *Ditrupa* (as *Ditrypa*) to be "abundant" off Shetland, from dredgings made around the islands in 1867 and 1868, but without quantification. Since he lists some other species as "very abundant" it is here considered that these densities of *Ditrupa* were not exceptional. McIntosh (1923) also recorded the species as abundant, but as he cited Crawshay (1912), who reported a single specimen from the western English Channel, again it is concluded that the densities were not particularly high.

Le Danois (1948) described a "facies à Dentales" from around the shelf edge of the Celtic Sea and off North Gascony with the scaphopod *Dentalium* and solitary coral *Caryophyllia* listed as characteristic taxa. In his list of the fauna of the shelf edge facies, *Ditrupa* was included (along with several other serpulid taxa) under 'epifauna'; *Ditrupa* was also included in lists of the principal fauna of the muddy facies of the Atlantic slope and of the semi-abyssal zone. In Supplement 1 to Le Danois's book, *Ditrupa* was not indicated to be either a facies characterising or a most important species, suggesting that it had not been found in great abundance.

Glémarec (1969) summarised the benthic faunal communities present off the North Gascony coast and mapped (his Fig. 1) a broad area of the outer Armorican shelf as comprising *Ditrupa* sands ("sables à alènes"). These were described as "sables roux à pointes d'alènes" with a median diameter of 270–400 μm and a zoogenic calcium carbonate content of >50%. Glémarec (1969) included (his Fig. 2) a seabed photo showing numerous *Ditrupa* tubes but did not give densities. The community was considered equivalent to the facies "à Dentales de la bordure continentale" distinguished by Le Danois (1948). This could be a suggestion that Le Danois's "Dentales" also included *Ditrupa*, although the difference could also reflect a major increase in *Ditrupa* densities in the decades between the surveys. Glémarec (1973), in his consideration of the European North Atlantic shelf benthic communities, included similar information on the *Ditrupa arietina/Dentalium entalis* community (of open sea étage fine sands) to that in Glémarec (1969) and Le Danois (1948) but again without densities; surprisingly, Stephen's (1923) report of a *Ditrupa* community widespread off Shetland was not cited.

A survey of the benthic fauna of the Celtic Sea was undertaken in 1974 and 1975 with the results given in a limited circulation report (Hartley and Dicks, 1977) and mollusc records published by Hartley (1979). *Ditrupa* was present at 20 of 86 stations sampled, with very high densities found at three sites off south-west (SW) Ireland sampled in May/June 1975 from the *RV Challenger*, summarised in table 1. The trawl at station C27 recovered some 14,800 live *Ditrupa*, and previously unpublished quantitative data from two 0.1m^2 grab samples from station C26 are given in table 2, where *Ditrupa* comprised 84% of the fauna retained on a 1mm mesh.

The fauna from the trawl at station C31 suggests some temporal persistence of the population, with a mix of living *Ditrupa* and vacated tubes occupied by other species or living on them. Of the 624 *Ditrupa* tubes retained by the trawl, 173 (28%) contained live *D. arietina*, 214 (34%) contained the amphipod *Siphonoecetes striatus* and 22 (4%) contained the sipunculan *Phascolion strombus*. In total, over 50% of empty tubes were occupied by other taxa, and the tubes frequently had the coral *Caryophyllia smithii* (35, 6%) or the serpulid *Hydroides norvegica* (18, 3%) attached. These observations and others (e.g. Gambi and Jerace, 1997; Morton and Salvador, 2009 ; Ferrero-Vicente et al., 2014) emphasise the importance of living and empty *Ditrupa* tubes as a habitat. The high densities of *Ditrupa* at some Celtic Sea stations were also noted by Dicks and Hartley (1982); they commented that the reasons for the establishment of such high-density, low-diversity communities in shelf depths were unclear.

Wilson (1982) suggested that *Ditrupa arietina* was the most important indicator species characteristic of the rippled sands of the ocean-facing outer continental shelf in the weak current areas of the western Celtic Sea and to the west of Brittany and Scotland. He noted that data on the density and distribution of *Ditrupa* were sparse, although to the west of Scotland the species occurred in discrete patches with densities of up to 1600/m^2. Wilson et al. (1983) obtained "several thousand live *Ditrupa*" from an anchor box dredge sample taken in September 1979 from a sand patch ~59 km west of the Hebrides. Dyer et al. (1982) noted and illustrated with a seabed photo taken in 1978, high densities of *Ditrupa* to the west of Shetland and indicated that *Ditrupa* and the echinoid *Cidaris* were characteristic of the area. Cranmer et al. (1984) also reported that *Ditrupa* was common and locally abundant in the area.

A stratified random regional survey of the East Shetland Basin of the North Sea was undertaken in July 2007 with samples obtained by 0.1m^2 Day grab from 86 stations (Hartley Anderson Ltd, 2008). *Ditrupa* was present at 24 stations, typically at low densities, but at stations 26, 28 and 40 it numerically dominated the fauna retained on a 1mm mesh (see tables 3, 4, 5 and 6 and fig. 2).

The two stations (26 and 28) with the highest densities of *Ditrupa* are species-rich and have an abundant fauna, with above survey average S (110 taxa) and N (909 individuals/0.1 m^2, n = 69). Thus the fauna is not high density, low diversity, as found in the NW Mediterranean (H' of ~2.5, Labrune et al., 2007a) and in the Celtic Sea (table 2). This suggests that in the northern North Sea at least, dense populations of *Ditrupa* can establish (by larval settlement and/or post larval redistribution) in the presence of an existing and diverse fauna, and in the presumed absence of significant physical disturbance. In addition, the station 26 and 28 results indicate that the presence and feeding activities of *Ditrupa* do not lead to a significant loss of diversity in the other fauna. The numerically important taxa listed in tables 5 and 6 show a good degree of commonality

Table 1. Details of high *Ditrupa* density stations in the Celtic Sea (Hartley and Dicks, 1977).

Station number	Sampling gear	Location	Depth (m)	Sediment type (visual observation)
C26	Agassiz trawl 0.1 m^2 Day grab (x2)	50°51'48"N 08°29'18"W	113	Muddy sand
C27	Agassiz trawl	50°57'54"N 08°42'0"W	110	Mud, sand, gravel, shells
C31	Agassiz trawl 0.1 m^2 Day grab	50°42'12"N 09°17'48"W	126	Sand, shells

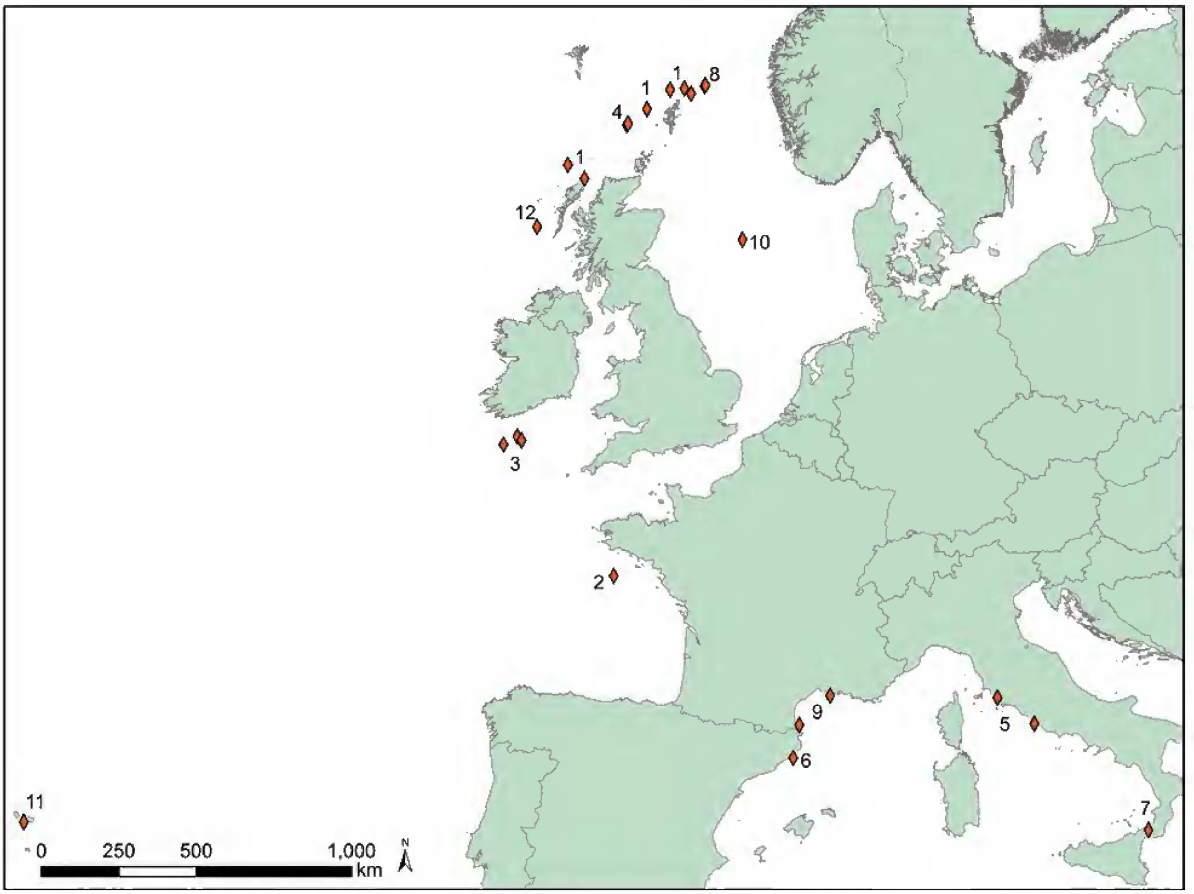

Figure 1. Records of high densities of *Ditrupa* from the North-east Atlantic and Mediterranean Sea. 1, Stephen (1923). 2, Glémarec (1969). 3, Hartley and Dicks (1977). 4, Dyer et al. (1982). 5, Gambi and Giangrande (1986). 6, Grémare et al. (1998). 7, Cosentino and Giacobbe (2006). 8, Hartley Anderson Ltd (2008). 9, Labrune et al. (2007a). 10, Gardline (2009). 11, Morton and Salvador (2009). 12, Wilson et al. (1983).

between stations (particularly stations 26 and 28, which clustered at >70% similarity in classification analysis) (Hartley Anderson Ltd, 2008). The use of 0.5mm and 1mm sieves results in some differences in the lists of numerically important taxa, but regardless of mesh size and the presence of juveniles, especially in the 0.5mm sieve data, the faunal dominance of *Ditrupa* is evident at stations 26, 28 and 40. The occurrence in abundance of the solitary coral *Caryophyllia smithii* where numerous *Ditrupa* tubes are present agrees with the findings of Wilson (1976).

Table 2. Total fauna from two 0.1m² grab samples from Celtic Sea survey station C26 (see Hartley and Dicks, 1977; nomenclature has been updated).

Station C26	Grab 1	Grab 2
Ditrupa arietina	377	741
Myriochele spp. agg.	41	52
Echinoidea juv.	2	19
Anthozoa juv.	3	10
Echinocyamus pusillus	2	9
Siphonoecetes striatus	1	9
Ophiura affinis	–	9
Phaxas pellucidus	2	7
Ophiuridae juv.	–	8
Aspidosiphon muelleri	2	5
Abra nitida	2	5
Hilbigneris gracilis	4	1
Amphictene auricoma	1	2
Owenia fusiformis	2	1
Amphipoda indet.	1	2
Ampelisca indet.	–	3
Ampharetidae juv.	–	3
Magelona sp.	2	–
Paranymphon spinosum	–	1
Atelecyclus rotundatus	1	–
Corbula gibba	–	1
∑/0.1 m²	446	885

Seabed photos taken at a site at 75 m depth in the central North Sea showed numerous *Ditrupa* tubes lying on the sediment surface (Gardline 2009, site JRP). Grab samples at the site indicated a *Ditrupa* density of 390/m² in moderately sorted fine sand with a mean grain size of 157 μm and a silt/clay content of 6.7% (ERT, 2009). This is considered to be a small patch of *Ditrupa*, as photos and samples from 16 other stations within 8 km showed the species to be absent or rare, which is consistent with the results of numerous macrofaunal surveys in the region (Rees et al., 2007, UK Benthos database and unpublished data).

Morton and Salvador (2009) reported *Ditrupa* at ~100–250 m depth off the Azores, and as a significant component of the fauna at depths of ~200 m; the samples were taken by dredge and quantitative density information was not included. They highlighted the different depth zones of *Ditrupa* occurrence between the Mediterranean and the Azores and suggested this may be related to differences in light penetration or food availability, or other factors such as sediment type or disturbance. Morton and Salvador (2009) also illustrate (their Fig. 4A[1]) and describe the live position of the worm (with the majority of the tube buried in the sediment) and indicate that, when placed on sediment, worms attempt to re-burrow. This contrasts with the range of published seabed photographs showing tubes lying at the sediment surface and would call into question the findings of Guizien et al. (2010) of *Ditrupa* spatial redistribution caused by swell-induced bed load transport.

Ellis et al. (2002, 2013) in a regional beam trawl study of the epifauna of the Celtic Sea noted that *Ditrupa* was very abundant at a number of sites and that it "was abundant off south-western Ireland at depths of 102–305 m". Ellis et al. (2002) listed *Ditrupa* in the dominant fauna associated with a *Pagurus prideaux–Porania pulvillus* assemblage of the southern Celtic Sea; a similar assemblage and its occurrence was described by Ellis et al. (2013), although *Ditrupa* was not listed in the dominant fauna.

Selected UK and North Sea areas where *Ditrupa arietina* is absent

Based on detailed regional surveys, it is apparent that *Ditrupa* is absent from some areas, such as the southern North Sea (Degraer et al., 2006; Daan and Mulder, 2006; Diesing et al., 2009; Tappin et al., 2011) and the Irish Sea (Bruce et al., 1963; Mackie et al., 1995; Robinson et al., 2009; Hartley Anderson Ltd, 2009). These areas coincide with non-stratified waters or areas of shallow stratification and suggest that in the North Atlantic *Ditrupa* is restricted to Glémarec's (1973) open sea étage, where annual thermal variations are small; this is in apparent contrast to the situation in the NW Mediterranean, where dense populations of *Ditrupa* are found in shallow 10–30 m coastal waters where bottom water temperatures have an ~10°C annual variation (Charles et al., 2003, their Fig. 9). Regional epifaunal surveys of the North Sea undertaken using beam trawls (Jennings et al., 1999; Callaway et al., 2002) did not report *Ditrupa*, even in areas of known occurrence; this is believed to reflect the sampling method.

Mediterranean records of high densities of *Ditrupa arietina*

Ditrupa was historically considered to be an uncommon species in the Mediterranean, although a dramatic increase in abundance along the NW Mediterranean coast occurred around 30 years ago. Grémare et al. (1998) reported high densities (>1000/m²) of *Ditrupa arietina* at all sites sampled in surveys off the Catalan coast carried out in the 1990s, with maximum densities of 11,086/m², accounting for as much as 79% of total macrofaunal abundance and biomass. *Ditrupa* was predominantly found in depths of between 20 and 30 m in well-sorted fine sands and muddy sands. Grémare et al. (1998) concluded that *Ditrupa* abundance had recently increased all along the Catalan coast (as there were few reports of the species in the area before 1970) and that the increase was not due to sediment instability but rather to a reduction in silt/clay in the sediment due to increased frequency of easterly storms. Sardá et al. (2000) also reported a significant increase in *Ditrupa* numbers in a shallow water area off the mouth of the Tordera River (Catalan coast) following the removal of sand by suction dredging for beach replenishment. The dredging defaunated the sediments and changed their grain size composition; fine sands redistributed over the winter after cessation of dredging and in spring were densely colonised by a range of species, including *Ditrupa*, which attained densities of ~2800/m².

Table 3. Details of the highest *Ditrupa* density stations in the northern North Sea (Hartley Anderson Ltd, 2008).

Station number	Location	Depth (m)	Sediment type	S[a]	N[a]	H'(log_2)	*Ditrupa* % of total fauna
26	61.216492° N 0.795038° E	166	Very poorly sorted fine sand	119	1093	4.9	43 (1 mm) 22 (0.5 + 1 mm)
28	61.236048° N 0.855043° E	167	Very poorly sorted fine sand	128	1222	4.8	49 (1 mm) 26 (0.5 + 1 mm)
40	61.024875° N 0.750020° E	156	No data	85	472	5.1	23 (1 mm) 12 (0.5 + 1 mm)
42	60.999035° N 0.618103° E	151	Poorly sorted fine sand	90	615	5.2	2 (1 mm) 3 (0.5 + 1 mm)

[a]Numbers from 0.1 m^2 sieved on 0.5mm mesh

Table 4. Sediment characteristics for highest *Ditrupa* density stations in the northern North Sea (Hartley Anderson Ltd, 2008)

Station	Carbonate %	Organic %	Mean diameter (μm)	Coarse % (>2 mm)	Fine % (<63 μm)	Silt %	Clay %
26	30.99	0.94	141	2.19	15.86	11.79	4.07
28	30.09	0.73	159	1.64	14.76	11.04	3.72
42	30.43	0.56	240	0.21	6.98	4.67	2.31

Figure 2. Photo of East Shetland Basin survey station 28 sample with numerous *Ditrupa* tubes; also visible are the solitary coral *Caryophyllia smithii* (red arrow) and the foraminiferan *Astrorhiza arenaria* (yellow arrow).

Table 5. The ten most abundant taxa (by rank) in metazoan fauna >0.5 mm at the highest *Ditrupa* density stations in the northern North Sea. Densities are numbers per 0.1 m^2 (Hartley Anderson Ltd, 2008).

Station 26 ∑1093/0.1 m^2		**Station 40 ∑472/0.1 m^2**	
Ditrupa arietina	243	*Ditrupa arietina*	56
Minuspio cirrifera	146	*Aricidea wassi*	49
Ophiura affinis	100	*Minuspio cirrifera*	47
Spiophanes kroyeri	45	*Spiophanes kroyeri*	41
Euchone sp. 1	44	*Myriochele* spp. agg.	26
Echinocardium juv.	44	*Owenia fusiformis*	17
Aricidea wassi	28	*Spiophanes bombyx*	14
Eclysippe cf. *vanelli*	28	*Echinocyamus pusillus*	14
Axinulus croulinensis	27	*Poecilochaetus serpens*	11
Glycera lapidum	21	*Glycinde nordmanni*	10
		Aonides paucibranchiata	10
		Ampharetidae juv.	10
		Echinocardium juv.	10
Station 28 ∑1222/0.1 m^2		**Station 42 ∑615/0.1 m^2**	
Ditrupa arietina	322	*Minuspio cirrifera*	64
Minuspio cirrifera	174	*Myriochele* spp. agg.	61
Ophiura affinis	94	*Aricidea wassi*	44
Echinocardium juv.	42	*Ophiura affinis*	44
Spiophanes kroyeri	35	*Echinocardium* juv.	35
Eclysippe cf. *vanelli*	31	*Spiophanes kroyeri*	33
Ampharetidae juv.	28	*Owenia fusiformis*	33
Axinulus croulinensis	25	*Euchone* sp. 1	19
Mugga wahrbergi	24	*Ditrupa arietina*	18
Polynoidae juv.	17	*Echinocyamus pusillus*	18
Myriochele spp. agg.	16		
Paraonides sp. 1	16		
Euchone sp. 1	16		

Table 6. The ten most abundant taxa (by rank) in metazoan fauna >1.0 mm at the highest *Ditrupa* density stations in the northern North Sea. Densities are numbers per 0.1 m^2 (Hartley Anderson Ltd, 2008).

Station 26 ∑562/0.1 m^2		**Station 40 ∑242/0.1 m^2**	
Ditrupa arietina	243	*Ditrupa arietina*	56
Ophiura affinis	47	*Spiophanes kroyeri*	27
Echinocardium juv.	42	*Owenia fusiformis*	15
Spiophanes kroyeri	31	*Spiophanes bombyx*	13
Minuspio cirrifera	20	*Echinocardium* juv.	10
Euchone sp. 1	17	*Echinocyamus pusillus*	9
Eclysippe cf. *vanelli*	14	*Minuspio cirrifera*	8
Caryophyllia smithii	12	Ampharetidae juv.	7
Glycera lapidum	6	*Euchone* sp. 1	6
Praxillella affinis	5	*Polydora* sp.	5
Polycirrus arcticus	5	*Urothoe elegans*	5
Cirolana borealis	5	*Yoldiella philippiana*	5
Eudorella truncatula	5		
Yoldiella philippiana	5		
Station 28 ∑659/0.1 m^2		**Station 42 ∑257/0.1 m^2**	
Ditrupa arietina	322	*Echinocardium* juv.	30
Ophiura affinis	55	*Owenia fusiformis*	27
Echinocardium juv.	42	*Ophiura affinis*	27
Spiophanes kroyeri	24	*Myriochele* spp. agg.	16
Caryophyllia smithii	16	*Spiophanes kroyeri*	15
Minuspio cirrifera	15	*Euchone* sp. 1	12
Eclysippe cf. *vanelli*	13	*Echinocyamus pusillus*	12
Polycirrus arcticus	9	*Minuspio cirrifera*	8
Yoldiella philippiana	9	*Chone longocirrata*	8
Ampharetidae juv.	7	*Spiophanes bombyx*	7
Euchone sp. 1	7	*Pseudopolydora paucibranchiata*	7
		Urothoe elegans	7

Medernach et al. (2000) investigated the ecology of these dense populations of *Ditrupa* and reported the species has a 2-year life span, starts breeding in its first year, has two spawning periods in a year, a planktonic larval stage lasting ~6 weeks, with high larval mortality on initial benthic settlement. Charles et al. (2003) extended these studies and found that settling larvae do not show sediment grain size selectivity, and concluded that the observed spatial heterogeneity in the density and structure of adult populations was mainly due to post-settlement processes. Charles et al. (2003) indicate a planktonic larval stage of 3 weeks (abstract) and ~4–5 weeks (text).

Labrune et al. (2007a), in a regional scale survey of the Gulf of Lions (NW Mediterranean), found from cluster analysis that *Ditrupa* was the numerically dominant polychaete in cluster I, comprising sands (fine to very fine sands with ~10% silt/clay from their Fig. 4) in 10–20m depth (average density of 616/m^2) and one of the dominants (average density of 100/m^2) in cluster IIa (stations in depths of 30 m in the west of the survey area, fine sands with ~20% silt/clay). Labrune et

al. (2007b) revisited the conclusions of Grémare et al. (1998) on the causes of increased *Ditrupa* abundance and proposed that they were in fact due to greater sediment stability linked to a reduction in the frequency of storms. Guizien et al. (2010) expanded the studies of these *Ditrupa* populations with field and lab flume experiments to investigate the hydrodynamic mobility of the animals in swell-induced currents. They found that normal tidal currents were not sufficient to transport animals with tubes >6 mm, but that moderate swell-induced currents could result in bed load transport of tubes of up to 25mm length. Field sampling before and after a swell event indicated hydrodynamic redistribution of animals, with significant losses or gains in densities of different size classes at some stations sampled; these changes were not linked to larval recruitment but to the translocation of adults. Guizien et al. (2010) considered that *Ditrupa* was epifaunal, without organs to allow burrowing or surface movement, was tolerant of sediment disturbance, and in shallow waters may not strictly be a sedentary species.

Dense populations of *Ditrupa* were reported from the Tyrrhenian Sea by Gambi and Giangrande (1986) and from its southeastern boundary (the Strait of Messina) by Cosentino and Giacobbe (2006). Gambi and Giangrande (1986) sampled around the mouths of the Rivers Tiber and Ombrone and listed *Ditrupa* as a characterising species in two station clusters: cluster C, comprising mixed sediments in water depths of 15–30 m off the Tiber, and cluster A, including fine and very fine sands in 5–10 m off the Ombrone. The samples were taken with a Charcot dredge, and their data are therefore considered semi-quantitative; the abundance data in their Table 1 are without area units. Cosentino and Giacobbe (2006) report high densities of *Ditrupa* (>500/0.25 m^2) in muddy sands (~20% mud) in depths of 35–45 m, where it made up nearly 80% of the polychaete and mollusc fauna. They variously describe the species as being eurytopic (an indicator of high sedimentation rates) and mud-tolerant. Cosentino and Giacobbe (2006) suggest several possible causes for the high *Ditrupa* density, including episodic high sediment load inputs as a result of terrestrial floods, and sediment disturbance/induced instability from pipeline installation. They note the transitory nature of the dense *Ditrupa* population found in their 1992 survey, with declines in abundance in the 1993 and 1995 surveys and an absence of living *Ditrupa* or dead tubes in 1999; this suggests that significant sediment movement(s) had occurred in the area, since complete empty tubes would be expected to endure for several years before fragmenting.

Discussion

The enigmatic discrepancies in the patterns of distribution and abundance of *Ditrupa* between the NE Atlantic and the Mediterranean raise a number of questions. In the NE Atlantic, the species has a wide distribution in waters that strongly stratify thermally (and is apparently absent from waters that do not and in more enclosed basins), with high densities typically found on ocean-facing outer continental shelves and upper slopes. In the Mediterranean, *Ditrupa* was considered uncommon until about 30 years ago but since then it has been widely recorded as a (or the) faunal dominant in shallow waters (typically ~10–30 m depth) of the NW Mediterranean and Tyrrhenian Sea.

This apparent ecological difference may point to the presence of two or more cryptic species, or the presence of an unrecognised introduced species in the Mediterranean. *Ditrupa* tube shape and free-living habit are distinctive and in routine surveys tend to be used for identification without examining the morphology of the worm inside. The Mediterranean examples examined by ten Hove and Smith (1990, from 40–50 m depth in the Baie de Cavalaire) consisted of empty tubes. Ten Hove and Kupriyanova (2009) note that the colour of the animals may be useful for serpulid species discrimination in the field but caution that there is inter- and intraspecific variability and that colour is rapidly lost in fixed material. Tantalisingly, there appears to be a difference in living *Ditrupa* branchial crown colouration from off Madeira (pallid in Fig. 1A in ten Hove and Kupriyanova, 2009) and those from the NW Mediterranean illustrated by Guizien et al. (2010, with red spots in their Fig. 1a). Investigations of the comparative morphology and genetics of specimens from the shallow Mediterranean and deeper NE Atlantic are now needed to resolve this enigma. The *Ditrupa* sequences currently in GenBank are all derived from Mediterranean material (from Banyuls, Kupriyanova et al., 2006; Kupriyanova and Rouse, 2008; and from Collioure, Lehrke et al., 2007).

An alternative explanation for the apparent ecological difference and absence from northern non-stratified waters is the thermal tolerance of the species, possibly in relation to winter minimum temperature, which in the southern North Sea can be ~4°C. Annual temperature variation seems an unlikely candidate, since Charles et al. (2003) illustrated an ~10°C range for the NW Mediterranean, which is similar to that recorded for the Celtic Sea.

There is a paucity of published detail on the sediment types occupied by dense *Ditrupa* populations, with a reported range from medium through very fine sands with a variable proportion of mud (<63 μm), to muds. However, sediment type may not be a key determining factor, based on the findings of Charles et al. (2003) that settling larvae do not show sediment grain size selectivity, and the density and structure of adult populations was mainly due to post-settlement processes.

Areas where dense populations of *Ditrupa* have been reported are subject to periodic sediment disturbance; in the shallow waters of the Mediterranean such disturbance has been attributed to storms (Grémare et al., 1998; Guizien et al., 2010), other physical processes, including strong tides, floodwaters and seismic activity (Cosentino and Giacobbe, 2006), or human activities such as sand extraction (Sardá et al., 2000) and pipeline installation (Cosentino and Giacobbe, 2006). In contrast, the areas of the NE Atlantic where abundant *Ditrupa* have been found are in water depths where storm-wave-induced oscillatory currents would not result in sediment disturbance (Draper, 1967) or be affected by strong tides, flood waters or seismic activity. Trawling is an additional source of sediment disturbance that could facilitate the establishment of high population densities of *Ditrupa* by disrupting elements of the existing benthic community.

However, in view of the extensive and long-term trawling that has occurred in the North Sea and the general absence of records of abundant *Ditrupa* in numerous benthic surveys, this does not appear to a major factor.

A source of sediment disturbance that does not seem to have been considered in previous discussions of dense *Ditrupa* populations is internal waves. These energetic phenomena are of global occurrence in waters with strong density gradients, and Jackson (2004) includes examples from all the areas considered earlier in this paper except the Tyrrhenian Sea. However, Nash and Moum (2005) identified river plumes as a source of internal waves, which indicates they could affect the areas studied by Gambi and Giangrande (1986). Pomar et al. (2012, see also Pomar et al., 2013) reviewed the major effects of internal waves on sediment mobilisation, structures and the sedimentary record. In the Celtic Sea (and Armorican shelf), the areas of high *Ditrupa* abundance appear to correspond with those influenced by internal waves, which occur during the summer months (July to September), when a well-developed thermocline is present (Pingree and Mardell, 1981; Jackson, 2004). Internal waves near the Celtic Sea shelf break have been observed to amplify spring barotropic tidal currents to in excess of 100 cm s^{-1} and may be important in modifying sediment transport rates (Heathershaw, 1985). As the Celtic Sea internal waves are seasonal, the sediment disturbance they cause may be an important factor in the establishment of dense populations of *Ditrupa*. Sediment disturbance may promote high *Ditrupa* densities in two ways: disruption of the established benthic fauna, allowing successful recruitment of large numbers of *Ditrupa* larvae; and through post-settlement redistribution and concentration in areas of deposition. The variability of internal wave occurrence, intensity and depth of impingement on the seabed (reflecting the variability of the seasonal and permanent pycnoclines) can be conjectured to explain why dense populations of *Ditrupa* near the shelf break appear to occur in patches rather than a continuous band. However, the Celtic Sea areas where *Ditrupa* occurs in abundance appear to be consistent with the near shelf break, where mixing by internal tide breaking results in a phytoplankton community dominated by picoeukaryotes and other larger phytoplankton, and which is distinct from that of adjacent oceanic and shelf areas (Green et al., 2008; Sharples et al., 2009). Sharples et al. (2009) indicate that the internal tide occurs regularly throughout the stratified season (April to September) and propose links to it, and its effects, on the timing of fish spawning, larval feeding, and the export of particulate organic matter out of the photic zone. Therefore, a possible alternative explanation for *Ditrupa* abundance in parts of the Celtic Sea is the seasonally enhanced food supply (plankton-derived particulate organic matter), which the life history of the species allows it to exploit effectively through post-larval redistribution into areas of particulate organic matter settlement. Charles et al. (2003) indicate that in the NW Mediterranean, the great bulk of *Ditrupa* larval settlement occurs in April to May (the spawning period in the NE Atlantic), and the environmental cues triggering it are not known, but, based on water temperatures, later spawning in the Celtic Sea can be conjectured.

Other NE Atlantic shelf edge areas and islands where dense populations of *Ditrupa* have been reported also develop seasonal thermoclines, have permanent thermoclines or have pycnoclines at the interface between different water masses. Therefore, sediment disturbance through internal wave breaking is proposed as a likely major contributory factor to the occurrence of such populations, potentially also linked to seasonal enhancement of plankton-derived food supply. The maps illustrating shelf edge surface chlorophyll peaks around the British Isles in Pingree and Mardell (1981, their plates 1 and 2) and Sharples et al. (2009, their Fig. 1) indicate areas of search for dense *Ditrupa* populations in future sampling exercises.

There do not appear to be any published time-series of benthic surveys of NE Atlantic areas where dense *Ditrupa* populations have been found. As a consequence, much of this discussion has relied on extrapolation from shallow-water Mediterranean evidence, which may not be applicable to deeper waters of the outer shelf and upper continental slope. Repeated sampling is required to better document the ecology of NE Atlantic *Ditrupa* populations and their role in characterising the benthic assemblages of the continental shelf. The different sampling methods used are a confounding variable in perspectives on benthic assemblages with *Ditrupa*. In particular, the sieve mesh used influences perceptions of the species composition and relative diversity of associated fauna (compare Stephen's (1923) results from a ~1.5 mm sieve with those from 1.0mm and 0.5mm meshes in tables 5 and 6 above). Similarly, trawl samplers may not retain *Ditrupa* unless they clog with sediment or have a fine mesh liner; thus it is uncertain if *Ditrupa* was not common in the wide area of the northern North Sea surveyed by Basford et al. (1989) or just not sampled. Eleftheriou and Basford (1989) did not include uncommon taxa in the interpretation of their regional grab survey of the northern North Sea, and since *Ditrupa* was not mentioned, it is assumed that it was not abundant in their samples. Seabed photography is valuable in documenting *Ditrupa* presence and density, ideally augmented with physical sampling to allow distinction between live animals and empty tubes. It is not known whether the difference in relative faunal diversity apparent between samples from the Celtic Sea (table 2) and northern North Sea (table 3) is real or a reflection of the low number of samples and differences in sample processing methods in the field; further sampling is required to enable valid comparisons to elucidate this.

This review aimed to conclude whether benthic assemblages dominated by *Ditrupa* were sufficiently consistent in their occurrence to warrant inclusion in habitat classifications, or alternatively, whether they were ephemeral and thus rightly excluded. For the NE Atlantic, the weight of evidence (albeit limited) suggests that dense populations of *Ditrupa* occur with sufficient regularity in areas with well-bounded depth and hydrodynamic conditions that the assemblage should be included in habitat classifications. Such classification schemes would benefit from revision to take account of internal waves as a significant source of bed shear stress, sediment disturbance and trophic modification in the deep circalittoral and upper slope, areas currently defined as where the seabed is not affected by waves. Considerable effort

has recently been expended to improve European habitat classifications for use in marine spatial planning and identification of marine protected areas (West et al., 2010; McBreen et al., 2011; Cameron and Askew, 2011), but none makes any reference to internal waves. This is remarkable since they have long been documented, together with their links to ecologically important habitats such as cold water corals (Frederiksen et al., 1992) and to sediment disturbance (Heathershaw, 1985; Hosegood and van Haren, 2004).

In addition, the ecology of *Ditrupa* presents a number of interesting questions. Is its free-living habit (in contrast to most other serpulids) an adaptation that allows colonisation of sedimentary areas, particularly those subject to periodic hydrodynamic disturbance, with the robust elephant tusk shaped tube allowing successful post larval and adult animal redistribution via bed-load transport, and facilitating both filter and surface deposit feeding? Is the operculum used by an animal to allow some repositioning or as an anchor in periods of high bed shear stress? Does the resulting spatially and temporally variable patchwork of *Ditrupa* densities hinder the establishment of high densities of predators such as naticid gastropods, or parasites?

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References

Basford, D.J., Eleftheriou, A., and Raffaelli, D. 1989. The epifauna of the northern North Sea (56°–61°N). *Journal of the Marine Biological Association of the United Kingdom* 69: 387–407.

Bruce, J.R., Colman, J.S., and Jones, N.S. (eds) 1963. *Marine fauna of the Isle of Man and its surrounding seas*, 2nd edn. Liverpool University Press: Liverpool, UK. 307 pp.

Callaway, R., Alsvåg, J., de Boois, I., Cotter, J., Ford, A., Hinz, H., Jennings, S., Kröncke, I., Lancaster, J., Piet, G., Prince, P., and Ehrich, S. 2002. Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES Journal of Marine Science* 59: 1199–1214.

Cameron, A., and Askew, N. (eds) 2011. *EUSeaMap – preparatory action for development and assessment of a European broad-scale seabed habitat map final report*. Available at http://jncc.gov.uk/euseamap

Charles, F., Jordana, E., Amouroux, J.M., Grémare, A., Desmalades, M., and Zudaire, L. 2003. Reproduction, recruitment and larval metamorphosis in the serpulid polychaete *Ditrupa arietina* (O.F. Müller). *Estuarine, Coastal and Shelf Science* 57: 435–443.

Cosentino, A., and Giacobbe, S. 2006. A case study of mollusc and polychaete soft-bottom assemblages submitted to sedimentary instability in the Mediterranean Sea. *Marine Ecology* 27: 170–183.

Cranmer, G.J., Dyer, M.F., and Fry, P.D. 1984. Further results from headline camera surveys in the North Sea. *Journal of the Marine Biological Association of the United Kingdom* 64: 335–342.

Crawshay, L.R. 1912. On the fauna of the outer-western area of the English Channel. *Journal of the Marine Biological Association of the United Kingdom* 9: 292–393.

Daan, R., and Mulder, M. 2006. *The macrobenthic fauna in the Dutch sector of the North Sea in 2005 and a comparison with previous data*. NIOZ-report 2006–3, NIOZ: Texel, The Netherlands. 93 pp.

Degraer, S., Wittoeck, J., Appeltans, W., Cooreman, K., Deprez, T., Hillewaert, H., Hostens, K., Mees, J., Vanden Berghe E., and Vincx, M. 2006. *The macrobenthos atlas of the Belgian part of the North Sea*. Belgian Science Policy. D/2005/1191/3. 164 pp.

Dicks, B., and Hartley, J.P. 1982. The effects of repeated small oil spillages and chronic discharges. *Philosophical Transactions of the Royal Society of London B* 297: 285–307.

Diesing, M., Ware, S., Foster-Smith, R., Stewart, H., Long, D., Vanstaen, K., Forster, R., and Morando, A. 2009. *Understanding the marine environment – seabed habitat investigations of the Dogger Bank offshore draft SAC*. JNCC Report No. 429. Joint Nature Conservation Committee: Peterborough, UK. 89 pp. +5 appendices.

Dominici, S. 2001. Taphonomy and paleoecology of shallow marine macrofossil assemblages in a collisional setting (late Pliocene–early Pleistocene, western Emilia, Italy). *Palaios* 16: 336–353.

Draper, L. 1967. Wave activity at the sea bed around northwestern Europe. *Marine Geology* 5: 133–140.

Dyer, M.F., Fry W.G., Fry P.D., and Cranmer, G.J. 1982. A series of North Sea benthos surveys with trawl and headline camera. *Journal of the Marine Biological Association of the United Kingdom* 62: 297–313.

Eleftheriou, A., and Basford, D.J. 1989. The macrobenthic infauna of the offshore northern North Sea. *Journal of the Marine Biological Association of the United Kingdom* 69: 123–143.

Ellis, J.R., Lancaster, J.E., Cadman, P.S., and Rogers, S.I. 2002. The marine fauna of the Celtic Sea. Pp. 45–65 in: Nunn, J.D. (ed.), *Marine biodiversity in Ireland and adjacent waters*. Ulster Museum: Belfast.

Ellis, J.R., Martinez, I., Burt, G.J., and Scott, B.E. 2013. Epibenthic assemblages in the Celtic Sea and associated with the Jones Bank. *Progress in Oceanography* 117: 76–88.

ERT. 2009. *ConocoPhillips Jasmine Field, pipeline route to Judy and new JRP site at Judy*. UKCS Blocks 30/06a and 30/07a. Environmental Baseline Survey, March 2009. ERT Report No. 2022.

European Environment Agency. EUNIS (European Nature Information System). http://eunis.eea.europa.eu/about.jsp

Ferrero-Vicente, L.M., Marco-Méndez, C., Loya-Fernández, A., and Sánchez-Lizaso, J.L. 2014. Observations on the ecology and reproductive biology of the sipunculan worm *Aspidosiphon muelleri* in temperate waters. *Journal of the Marine Biological Association of the United Kingdom* 94: 1629–1638.

Frederiksen, R., Jensen, A., and Westerberg, H. 1992. The distribution of the Scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. *Sarsia* 77: 157–171.

Gambi, M.C., and Giangrande, A. 1986. Distribution of soft-bottom polychaetes in two coastal areas of the Tyrrhenian Sea (Italy): structural analysis. *Estuarine, Coastal and Shelf Science* 23: 847–862.

Gambi, M.C., and Jerace, S. 1997. Epibiosis on the tubes of the polychaete *Ditrupa arietina* Serpulidae in some populations of the soft bottoms off the southern Tyrrhenian Sea. *Biologia Marina Mediterranea* 4: 380–383.

Gardline. 2009. *Jasmine to Judy export pipeline corridor route and environmental baseline surveys*. UKCS Block 30/06a and 30/07a. Pipeline Route Survey Report. Gardline Project Ref. 7987. Report by Gardline Geosurvey Ltd, Great Yarmouth.

Glémarec, M. 1969. Le plateau continental Nord-Gascogne et la Grande Vasière étude bionomique. *Revue des Travaux Institut des Pêches Maritimes* 33: 301–310.

Glémarec, M. 1973. The benthic communities of the European North Atlantic continental shelf. *Oceanography and Marine Biology: an Annual Review* 11: 263–289.

Green, J.A.M., Simpson, J.H., Legg, S., and Palmer, M. 2008. Internal waves, baroclinic energy fluxes and mixing at the European shelf edge. *Continental Shelf Research* 28: 937–950.

Grémare, A., Sardá, R., Medernach, L., Jordana, E., Pinedo, S., Amouroux, J.M., Martin, D., Nozais, C., and Charles, F. 1998. On the dramatic increase of *Ditrupa arietina* O.F. Müller (Annelida: Polychaeta) along both the French and the Spanish Catalan coasts. *Estuarine, Coastal and Shelf Science* 47: 447–457.

Grey, M., Boulding, E.G., and Brookfield, M.E. 2005. Shape differences among boreholes drilled by three species of naticid gastropods. *Journal of Molluscan Studies* 71: 253–256.

Guizien, K., Charles, F., Hurther, D., and Michallet, H. 2010. Spatial redistribution of *Ditrupa arietina* (soft bottom Mediterranean epifauna) during a moderate swell event: evidence and implications for biotic quality indices. *Continental Shelf Research* 30: 239–251.

Hartley Anderson Ltd. 2008. *2007 East Shetland Basin Regional Survey*. Hartley Anderson Ltd. Report HAL/O&GUK/ 2008.9 to the Government/Industry Offshore Environmental Monitoring Committee. 25 pp. + appendices.

Hartley Anderson Ltd. 2009. *2008 Irish Sea regional survey data*. Hartley Anderson Ltd. report HAL/O&GUK/ 2009.11 to the Government/Industry Offshore Environmental Monitoring Committee. 7 pp. + appendices.

Hartley, J.P. 1979. On the offshore Mollusca of the Celtic Sea. *Journal of Conchology* 30: 81–92.

Hartley, J.P., and Dicks, B.M. 1977. *Survey of the benthic macrofaunal communities of the Celtic Sea*. Oil Pollution Research Unit (Field Studies Council), Pembroke. 16 pp. + appendices.

Heathershaw, A.D. 1985. Some observations of internal wave current fluctuations at the shelf-edge and their implications for sediment transport. *Continental Shelf Research* 4: 485–493.

Hosegood, P.J., and van Haren, H. 2004. Near-bed solibores over the continental slope in the Faeroe–Shetland Channel. *Deep-Sea Research Part II* 51: 2943–2971.

Jackson, C. 2004. *An atlas of internal solitary-like waves and their properties*, 2nd edn. Prepared under contract with the Office of Naval Research, Code 322PO. http://www.internalwaveatlas.com/Atlas2_index.html

Jennings, S., Lancaster, J., Woolmer, A., and Cotter, J. 1999. Distribution, diversity and abundance of epibenthic fauna in the North Sea. *Journal of the Marine Biological Association of the United Kingdom* 79: 385–399.

Kupriyanova, E.K., McDonald, T.A., and Rouse, G.W. 2006. Phylogenetic relationships within Serpulidae (Annelida: Polychaeta) inferred from molecular and morphological data. *Zoologica Scripta* 35: 421–439.

Kupriyanova, E.K., and Rouse, G.W. 2008. Yet another example of paraphyly in Annelida: molecular evidence that Sabellidae contains Serpulidae. *Molecular Phylogenetics and Evolution* 46: 1174–1181.

Labrune, C., Grémare, A., Amouroux, J.M., Sardà, R., Joao, G., and Taboada, S. 2007a. Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. *Estuarine, Coastal and Shelf Science* 71: 133–147.

Labrune, C., Grémare, A., Guizien, K., and Amouroux, J.M. 2007b. Long-term comparison of soft bottom macrobenthos in the bay of Banyuls-sur-Mer (Northwestern Mediterranean Sea): a reappraisal. *Journal of Sea Research* 58: 125–143.

Le Danois, E. 1948. *Les profondeurs de la mer. Trente ans de recherches sur la faune sous-marine au large des côtes de France*. Payot: Paris. 303 pp.

Lehrke, J., ten Hove, H.A., Macdonald, T.A., Bartolomaeus, T., and Bleidorn, C. 2007. Phylogenetic relationships of Serpulidae (Annelida: Polychaeta) based on 18S rDNA sequence data, and implications for opercular evolution. *Organisms, Diversity & Evolution* 7: 195–206.

Mackie, A.S.Y., Oliver, P.G., and Rees, E.I.S. 1995. *Benthic biodiversity in the southern Irish Sea*. Studies in Marine Biodiversity and Systematics from the National Museum of Wales. BIOMÔR Reports 1. 263 pp.

Martinell, J., Kowalewski M., and Domènech, R. 2012. Drilling predation on serpulid polychaetes (*Ditrupa arietina*) from the Pliocene of the Cope Basin, Murcia region, Southeastern Spain. *PLoS ONE* 7(4): e34576.

McBreen, F., Askew, N., Cameron, A., Connor, D., Ellwood, H., and Carter, A. 2011. *UKSeaMap 2010: predictive mapping of seabed habitats in UK waters*. JNCC Report, No. 446. 103 pp.

McIntosh, W.C. 1869. Report on the Annelids dredged off the Shetland Islands by Mr. Gwyn Jeffreys in 1867–68. Pp. 231–345 in: Jeffreys, J.G., Norman, A.M., McIntosh, W.C. and Waller, E. (eds), *Last report on dredging among the Shetland Isles*. Report of the British Association for the Advancement of Science for 1868.

McIntosh, W.C. 1923. *A monograph of the British marine Annelids, Volume IV, Part II. Polychaeta – Sabellidae to Serpulidae with additions to the British marine Polychaeta during the publication of the monograph*. Ray Society. Pp. 251–538, 14 pls.

Medernach, L., Jordana, E., Grémare, A., Nozais, C., Charles, F., and Amouroux, J.M. 2000. Population dynamics, secondary production and calcification in a Mediterranean population of *Ditrupa arietina* (Annelida: Polychaeta). *Marine Ecology Progress Series* 199: 171–184.

Morton, B., and Salvador, A. 2009. The biology of the zoning subtidal polychaete *Ditrupa arietina* (Serpulidae) in the Açores, Portugal, with a description of the life history of its tube. *Açoreana Suplemento* 6: 145–156.

Müller, O.F. (1776) *Zoologiae Danicae Prodromus, seu animalium Daniae et Norvegiae indigenarum. Characteres, nomina et synonyma imprimis popularium*. Havniae, 1776, xxxii + 282 pp.

Myers, A.A., and McGrath, D. 1979. The British and Irish species of *Siphonoecetes* Kroyer (Amphipoda–Gammaridea). *Journal of Natural History* 13: 211–220.

Nash, J.D., and Moum, J.N. 2005. River plumes as a source of large-amplitude internal waves in the coastal ocean. *Nature* 437: 400–403.

Pingree, R.D., and Mardell, G.T. 1981. Slope turbulence, internal waves and phytoplankton growth at the Celtic Sea shelf-break. *Philosophical Transactions of the Royal Society of London A* 302: 663–682.

Pomar, L., Morsilli, M., Hallock, P., and Bádenas, B. 2012. Internal waves, an under-explored source of turbulence events in the sedimentary record. *Earth-Science Reviews* 111: 56–81.

Pomar, L., Morsilli, M., Hallock, P., Bádenas, B., and Bourgault, D. 2013. Reply to Shanmugam, G., comment on "Internal waves, an under-explored source of turbulence events in the sedimentary record". *Earth-Science Reviews* 116: 206–210.

Rae, B.B. 1956. The food and feeding habits of the lemon sole. *Marine Research* 1956(3): 1–32.

Rees, H.L., Eggleton, J.D., Rachor, E., and Vanden Berghe, E. (eds) 2007. *Structure and dynamics of the North Sea benthos*. ICES Cooperative Research Report No. 288. 258 pp.

Robinson, K.A., Darbyshire, T., Van Landeghem, K., Lindenbaum, C., McBreen, F., Creaven, S., Ramsay, K., Mackie, A.S.Y., Mitchell, N.C., Wheeler, A., Wilson, J.G., and O'Beirn, F. 2009. *Habitat mapping for conservation and management of the southern Irish Sea (HABMAP) I: seabed surveys*. Studies in Marine Biodiversity and Systematics from the National Museum of Wales. BIOMÔR Reports 5(1). 148 pp. + appendices.

Sardá, R., Pinedo, S., Grémare, A., and Taboada, S. 2000. Changes in the dynamics of shallow sandy-bottom assemblages due to sand extraction in the Catalan Western Mediterranean Sea. *ICES Journal of Marine Science* 57: 1446–1453.

Sharples, J., Moore, C.M., Hickman, A.E., Holligan, P.M., Tweddle, J.F., Palmer, M.R., and Simpson, J.H. 2009. Internal tidal mixing as a control on continental margin ecosystems. *Geophysical Research Letters* 36: L23603.

Stephen, A.C. 1923. Preliminary survey of the Scottish waters of the North Sea by the Petersen Grab. *Scientific Investigations of the Fisheries of Scotland 1922* III: 1–21.

Tappin, D.R., Pearse, B., Fitch, S., Dove, D., Geary, B., Hill, J., Chambers, C., Bates, R., Pinnion, C., Green, M., Gallyot, J., Georgiou, L., Brutto, D., Marzialetti, S., Hopla, E., Ramsay, E., and Fielding, H. 2011. *The Humber regional environmental characterisation*. British Geological Survey Open Report OR/10/54. 317 pp.

ten Hove, H.A., and Kupriyanova, E.K. 2009. Taxonomy of Serpulidae (Annelida, Polychaeta): the state of affairs. *Zootaxa* 2036: 1–126.

ten Hove, H.A., and Smith, R.S. 1990. A re-description of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a discussion of the genus. *Records of the Australian Museum* 42: 101–118.

West, N., Swift, R., and Bell, C. 2010. *Accessing and developing the required biophysical datasets and data layers for Marine Protected Areas network planning and wider marine spatial planning purposes*. Report No 10: Task 2E. Seabed Energy Layers. Available at http://randd.defra.gov.uk/Document.aspx?Document=MB0102_9939_TRP.pdf

Wilson, J.B. 1976. Attachment of the coral *Caryophyllia smithii* S. & B. to tubes of the polychaete *Ditrupa arietina* (Müller) and other substrates. *Journal of the Marine Biological Association of the United Kingdom* 56: 291–303.

Wilson, J.B. 1979. Biogenic carbonate sediments on the Scottish continental shelf and on Rockall Bank. *Marine Geology* 33: 85–93.

Wilson, J.B. 1982. Shelly faunas associated with temperate offshore tidal deposits. Pp. 126–171 in: Stride, A.H. (ed.), *Offshore tidal sands – processes and deposits*. Chapman and Hall: London.

Wilson, J.B. et al. 1983. *RRS Challenger Cruise 12/79: 18 August – 7 September 1979. Geological investigations in the northern North Sea and on the continental shelf west and north of Scotland; recovery and relaying of current meter moorings south and west of the Wyville–Thomson Ridge*. Institute of Oceanographic Sciences, Cruise Report No. 153, 22 pp.